Contrasting microclimates among hedgerows and woodlands across temperate Europe

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Declarations of interest: none.

Abstract

Hedgerows have the potential to facilitate the persistence and migration of species across landscapes, mostly due to benign microclimatic conditions. This thermal buffering function may become even more important in the future for species migration under climate change. Unfortunately, there is a lack of empirical studies quantifying the microclimate of hedgerows, particularly at broad geographical scales.

Here we monitored sub-canopy temperatures using 168 miniature temperature sensors distributed along woodland-hedgerow transects, and spanning a 1600-km macroclimatic gradient across Europe. First, we assessed the variation in the temperature offset (that is, the difference between sub-canopy and corresponding macroclimate temperatures) for minimum, mean and maximum temperatures along the woodland-hedgerow transects. Next, we linked the observed patterns to macroclimate temperatures as well as canopy structure, overstorey composition and hedgerow characteristics.

The sub-canopy versus macroclimate temperature offset was on average 0.10 °C lower in hedgerows than in woodlands. Minimum winter temperatures were consistently lower by 0.10 °C in hedgerows than in woodlands, while maximum summer temperatures were 0.80 °C higher, albeit mainly around the woodland-hedgerow ecotone. The temperature offset was often negatively correlated with macroclimate temperatures. The slope of this relationship was lower for maximum temperatures in hedgerows than in woodlands. During summer, canopy cover, tree height and hedgerow width had strong cooling effects on maximum mid-day temperatures in hedgerows. The effects of shrub height, shrub cover and shade-casting ability, however, were not significant.

To our knowledge, this is the first study to quantify hedgerow microclimates along a continental-scale environmental gradient. We show that hedgerows are less efficient thermal insulators than woodlands, especially at high ambient temperatures (e.g. on warm summer days). This knowledge will not only result in better predictions of species distribution across fragmented landscapes, but will also help to elaborate efficient strategies for biodiversity conservation and landscape planning.

Keywords: Climate change; fragmentation; macroclimatic gradient; species migration; temperature buffering; woody corridors

1. Introduction

Climate change is affecting a wide range of ecosystems and their biota across the globe, leading to phenological shifts ((Fitter and Fitter, 2002)), latitudinal and elevational range changes ((Lenoir and Svenning, 2015)) and evolutionary adaptations ((Hoffmann and Sgrò, 2011)). These effects are further aggravated by land-use changes ((Mantyka-Pringle et al., 2015)), leading to a range-wide increase in the extinction risk among threatened populations ((Jump and Penuelas, 2005)). In particular, habitat fragmentation is expected to impede the movements of species across the landscape, limiting their ability to closely track the shifting climatic envelopes. Strategies for improving landscape connectivity, for example, through the creation and maintenance of connecting habitats, will therefore be imperative to ensure the conservation of biodiversity under climate change ((Damschen et al., 2006)).

Woody corridors (e.g. hedgerows and linear woody habitats) are among the most common examples of connecting habitats ((Baudry et al., 2000)). On a regional scale, these corridors have been repeatedly identified as a substitute habitat ((McCollin et al., 2000; Van Den Berge et al., 2018)) or dispersal route ((Closset-Kopp et al., 2016; Tikka et al., 2001; Wehling and Diekmann, 2009)) for species within agricultural landscapes. Yet, at larger scales, the role of hedgerows as conservation corridors for woodland-dwelling communities is still debated, and some studies indicated that most specialist species will not benefit from hedgerows to facilitate their movements across the landscape ((Burel and Baudry, 1990; Liira and Paal, 2013; Wehling and Diekmann, 2008)). Indeed, many woodland specialists are slow colonizers ((Hermy et al., 1999; Verheyen et al., 2003)) and need a long time to disperse along linear woody habitats, in some cases even centuries ((Liira and Paal, 2013)). Besides, the establishment and persistence of woodland specialists in hedgerows might be severely hampered by their lower habitat quality ((de Blois et al., 2001; Liira and Paal, 2013; Roy and de Blois, 2006)). Hedgerows typically have higher soil nutrient levels, favouring the growth of highly competitive ruderal species at the expense of specialized forest species ((Wehling and Diekmann, 2009)). Their microclimate (i.e. sub-canopy local climate which is buffered and thus decoupled from the background climate or ‘macroclimate’; (Bramer et al., 2018)) also differs significantly from woodlands, with higher air mixing, increased incoming radiation and lower relative air humidity ((Honnay et al., 2005)).

Woodland microclimates have been abundantly studied (e.g. (Carlson and Groot, 1997; Chen et al., 1993; Chen et al., 1999; Morecroft et al., 1998; Renaud and Rebetez, 2009; von Arx et al., 2013)), and are the result of an interplay between several physical drivers (cf. (Barry and Blanken, 2016; Campbell and Norman, 1998; Geiger et al., 2009)). During the day, a large fraction of the incident solar radiation is absorbed or reflected by the leaves, needles and branches in the canopy. The amount of light reaching the woodland floor is largely governed by the leaf area index (LAI), leaf characteristics (size, shape, orientation and spectral properties) and canopy architecture. In particular, as the canopy becomes denser, more solar radiation is absorbed or reflected and less light penetrates into the woodland floor. To illustrate, dense woodlands absorb about 75-90 % of the incoming solar radiation ((Bonan, 2015)). Together with the effect of shading by the canopy, this causes lower ground-layer temperatures and a diminished sensible heat flux in woodlands compared to non-wooded lands. Conversely, most of the incoming solar energy is converted into latent heat via evapotranspiration, resulting in an additional cooling effect. On top of that, wind speeds are significantly reduced in woodlands due to the resistance with tree stems, branches and leaves, leading to a diminished mixing of air due to turbulence. As a result, less warm air is transported down into the woodland. During the night, the outgoing longwave (infrared) radiation from the ground surface and vegetation is partly reflected by the canopy, causing warmer night-time temperatures in woodlands compared to open lands ((Geiger et al., 2009; Morecroft et al., 1998)).

Hedgerow microclimates, on the other hand, are still poorly understood and the underlying physical processes are likely more complex due to the predominant influence of edge effects. For instance, depending on their spatial configuration in the landscape, hedgerows may considerably modify local wind speeds and turbulent mixing of air masses, which could in turn affect their microclimate ((Brandle et al., 2004; Heisler and Dewalle, 1988; McNaughton, 1988; Pasek, 1988)). Empirical studies with in-situ measurements of the sub-canopy conditions inside these woody corridors are thus urgently needed. These insights are particularly relevant from an ecological point of view because these conditions directly affect the ability of species to grow, survive, reproduce and disperse in hedgerows ((de Blois et al., 2002; Deckers et al., 2004a; Harvey et al., 2005)). Hedgerow microclimates may thus largely determine the ecological function of woody corridors for species (re-)distribution ((Deckers et al., 2004b; Sánchez et al., 2009)). To illustrate, Roy and de Blois

(2006) attributed the under-representation of early-flowering and late-maturing plant species in hedgerows of southern Quebec to the unfavourable sub-canopy climate therein, in particular the higher risk of late frosts in spring and early frosts in autumn. Hedgerow microclimates have also been shown to play an important role in governing the occurrence of several invertebrate species in agricultural areas ((Gardiner and Dover, 2008)), and may effectively contribute to the survival of birds and mammals, for example, by providing a shelter for these species during extreme climatic events ((Oliver et al., 2017; Pereira and Rodríguez, 2010)).

Furthermore, several recent studies have highlighted the role of microclimates in shaping species distribution under contemporary climate change ((Keppel and Wardell-Johnson, 2015); Suggitt et al., 2018). For instance, evidence suggests that tree canopies may effectively buffer understorey environments against climate extremes and support microclimates that may moderate the response of sub-canopy species to macroclimatic warming ((Davis et al., 2019; De Frenne et al., 2013; De Frenne et al., 2019; Lenoir et al., 2017)). Understanding and quantifying how micro-environmental conditions in hedgerows vary across space and time is thus key to predict species distribution patterns and colonization dynamics in linear habitats, particularly under an altering macroclimate. Yet, to our knowledge, a continental-scale characterization of hedgerow microclimates is still lacking.

To address this knowledge gap, we monitored sub-canopy temperatures using 168 miniature temperature sensors distributed along woodland-hedgerow transects, and spanning a 1600-km latitudinal gradient from northern France to central Norway. The macro-ecological gradient along which these sites were selected ensured that the large-scale climatic conditions of temperate Europe were adequately captured in our study. In each site, we recorded sub-canopy (microclimate) temperatures using six miniature data loggers spread across an edge-to-core gradient, and corrected these for the corresponding ambient free-air (macroclimate) temperatures obtained from weather stations. More specifically, we calculated the magnitude of the temperature offset for daily mean, maximum and minimum temperature values as microclimate temperatures minus macroclimate temperatures; negative values thus denote cooler temperatures below tree canopies, while positive values denote warmer understorey temperatures. We focus on temperature offsets rather than absolute values to facilitate among-region comparisons across Europe, because macroclimate-microclimate temperature differences are most relevant for species' responses to climate change, and because temporal temperature changes due to anthropogenic climate change are also expressed against a baseline. Next, we assessed the variation in the magnitude of the temperature offset along the woodland-hedgerow transects, and linked the observed patterns to ambient macroclimate temperatures as well as canopy structure and composition (canopy cover, height and total cover of shrub and tree layer, shade-casting ability) and hedgerow characteristics (hedgerow width and vertical structure). Finally, we also computed the diurnal temperature range for each sensor as daily maximum minus minimum temperatures, and related this to the same set of environmental variables.

Specifically, we tested the following hypotheses:

H1: Hedgerows provide lower buffering against temperature extremes than woodland interiors; maximum temperatures in hedgerows are higher than in adjacent woodland patches, while minimum temperatures are lower.

H2: The thermal buffering capacity of woodlands and hedgerows depends on ambient macroclimate temperatures.

H3: Temperature conditions inside hedgerows are governed by structural site characteristics such as canopy cover, tree height, corridor width, etc. In this regard, we expect that wider hedgerows with a taller and denser tree canopy are more effectively buffered against temperature extremes than narrower hedgerows with contrasting features.

Our study is unique in the sense that it is, to our knowledge, the first to quantify the sub-canopy microclimate of hedgerows at a continental extent. The outcomes of this study will help us to better understand and predict colonization dynamics of woodland-dwelling species in woody corridors, particularly in the face of climate change. Not only will this strengthen our ability to forecast future species distributions along linear habitats, but it will also contribute to more-informed landscape planning and conservation decision-making, including the preservation, establishment and management of connecting habitats in agricultural landscapes.

2. Materials and methods

2.1. Study area

This study was conducted in agricultural landscapes of seven regions spanning a latitudinal gradient of ca. 1600 km within the temperate forest biome of Europe (**Fig. 1a**). The mean annual temperature (MAT) across the study regions ranged from 5.18 (Tartü, Estonia) to 10.3 °C (Gontrode, Belgium) and the mean annual precipitation (MAP) from 606 (Tartü, Estonia) to 1066 mm (Trondheim, Norway) (long-term average values from 1970-2000 for MAT and MAP; (Fick and Hijmans, 2017)).

In each region, we selected four distinct sites of paired woodland-hedgerow combinations (**Table A.1**), located on a similar soil type (*Luvisol* or *Cambisol*; (IUSS Working Group WRB, 2015)) to maximize comparability. These sites were located at a median distance of 4 km from each other, but not closer than 1 km to avoid potential spatial autocorrelation effects. All hedgerows were at least 50 years old, structurally diverse (preferably with shrub and tree layer) and surrounded by open and treeless habitats (e.g. farmland, rotational grassland or road). Furthermore, the hedgerows were connected to an ancient woodland (here woodland that existed before 1850), whereof the canopy was mainly composed of broadleaf species. However, in regions with a hemi-boreal climate such as Estonia and Norway, a higher occurrence of coniferous species was unavoidable. Across all regions, the woodland canopies mainly consisted of *Fraxinus excelsior* (present in 31.0 % of all woodlands), *Fagus sylvatica* (23.8 %), *Carpinus betutlus* (17.9 %), *Quercus robur* (16.7 %) and *Acer pseudoplatanus* (15.5 %) (cf. **Table A.2** for an overview of the most dominant tree and shrub species in each of the study regions).

2.2. Microclimate and macroclimate

In this study, we considered sub-canopy microclimates to represent the small-scale climatic variations that are experienced by organisms living in the understorey of woody habitats such as forest-floor plants, small mammals, birds, insects, fungi, soil biota, etc. In general, these conditions comprise a wide range of climatic variables including temperature, precipitation, humidity and wind. Here we specifically focussed on sub-canopy temperatures given their role in modulating the response of biotic communities to macroclimatic warming ((De Frenne et al., 2013)). The macroclimate was defined as the climate of a large geographic area, which is characterized by a network of meteorological stations established in open-field conditions (e.g. in short grasslands, ca. 2 m above ground level), thus excluding the effect of woodland canopies (sensu (World Meteorological Organization, 2008)).

To quantify the microclimate in each woodland-hedgerow site, the air temperature was recorded at a two-hourly interval between September 1, 2017 and September 1, 2018 using miniature temperature sensors (type HOBO 8K Pendant Temperature/Alarm Data Logger – UA-001-08; accuracy at 0-50 °C: ±0.53 °C; resolution at 25 °C: 0.14 °C) installed exactly in the middle of the hedgerow. In each of the four sites within a given region, we deployed six temperature sensors along a hedgerow-to-woodland interior transect (**Fig. 1b**). All sensors were mounted in a radiation shield at 1 m height above the soil surface, attached to a tree trunk and oriented towards the north to avoid direct incoming solar radiation on the shield. For each sensor, we computed daily mean, minimum and maximum temperature values as well as the diurnal temperature range (daily maximum minus minimum temperature).

Macroclimate temperature data were obtained for each study site from nearby weather stations (using the following sources: Meteo France, Royal Meteorological Institute of Belgium, Deutscher Wetterdienst, Swedish Meteorological and Hydrological Institute, Estonian Weather Service and Norwegian Meteorological Institute; **Table A.3**). For each weather station, we extracted the daily mean, minimum and maximum temperature for the same period of September 1, 2017 to September 1, 2018.

2.3. Site characteristics

At each sensor location, canopy cover was estimated using a convex spherical crown densiometer (Forestry Suppliers, Model A), and calculated as the proportion of 96 points that was intersected by vegetation. In addition, we identified all woody species in the shrub (1-7 m) and tree layer (> 7 m) in a 2-m circular plot around each sensor (**Fig. 1c**), and estimated their percentage cover relative to the plot area. The height of the shrub and tree layer was determined with an ultrasound distance-measuring instrument (Haglöfs Vertex IV). The total cover of the shrub and tree layer was computed as the sum of the cover percentages of all individual species occurring these layers, allowing values to exceed 100 % due to overlaps. To characterize the canopy composition, we calculated the shade-casting ability (SCA) of all canopy species per plot (including both shrub and tree species) as the cover-weighted average of the SCA scores ((sensu Maes et al., 2019;

Verheyen et al., 2012)). These scores range between '1' (very low SCA) and '5' (very high SCA), and are listed for all canopy species in **Table A.4**. Both canopy structure and composition are expected to differ significantly between hedgerows and adjacent woodlands (see **Fig. A.1**), and will likely play a key role in explaining dissimilarities in microclimatic conditions between both habitat types. Finally, we also measured the width of the hedgerows as the perpendicular distance to the outermost edges of the shrub and tree crows (sensu (Corbit et al., 1999)) (**Fig. 1c**). The vertical structure was categorized visually as one-storied low, one-storied high, two-storied, multi-storied or diffuse (**Fig. 1d**). An overview of all inventoried site characteristics is given in **Table A.5**.

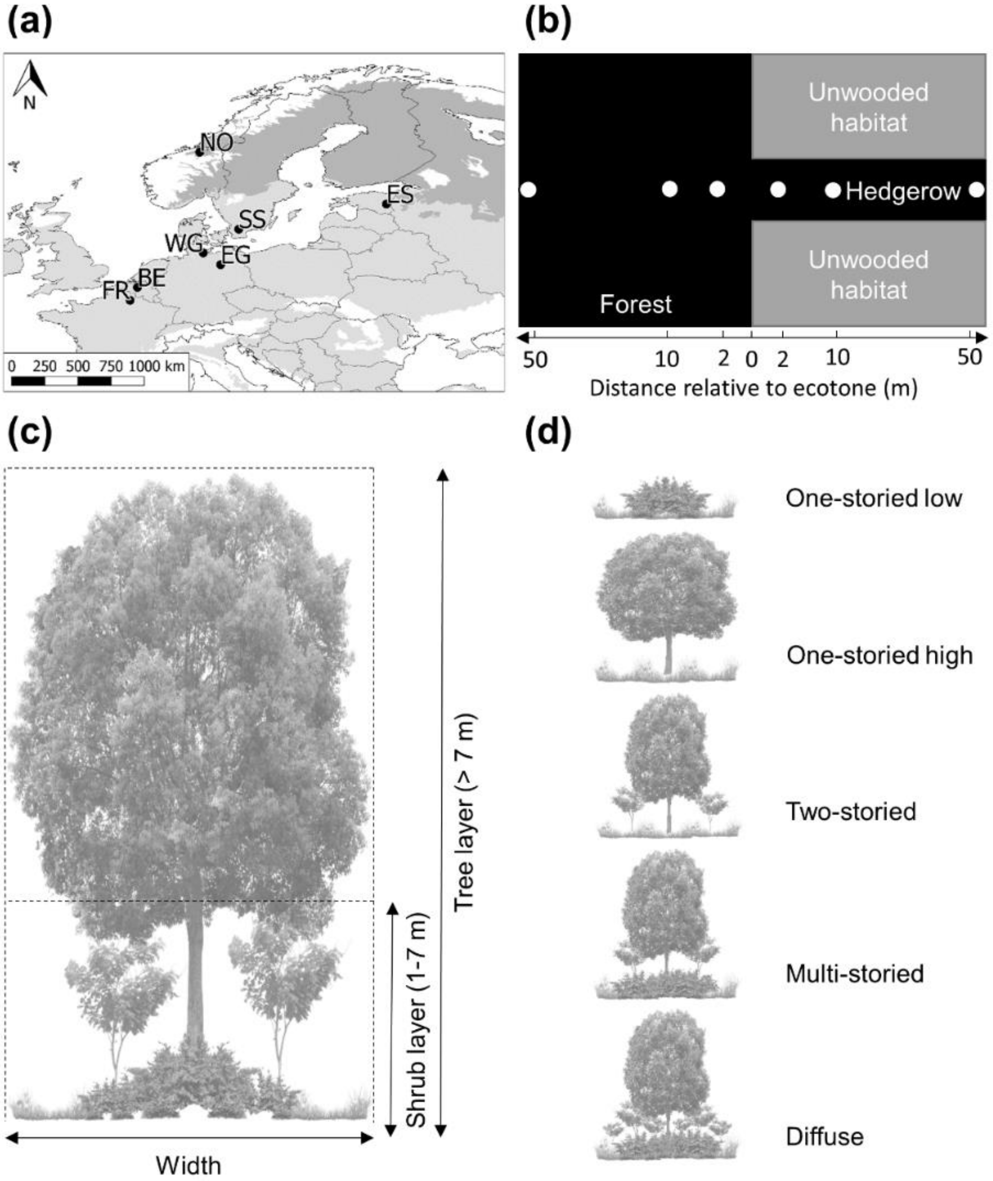

Fig. 1. Study area and experimental setup (a) Map showing the distribution of the seven study regions across Europe (Country codes: FR = France, BE = Belgium, WG = Western Germany, EG = Eastern Germany, SS = Southern Sweden, ES = Estonia, NO = Norway). The *light grey area* represents the temperate forest biome, while the *dark grey area* shows the boreal forest biome (following (Olson et al., 2001)) **(b)** Schematic representation of a study site, consisting of a hedgerow connected to an ancient woodland patch. Temperature sensors (*white circles*) were mounted at fixed distances (relative to the forest-hedgerow ecotone) along a transect going from 50 m inside the woodland patch towards 50 m along the hedgerow. This set-up was repeated four times per region. **(c)** Vertical profile of a hedgerow. Hedgerow width was measured as the distance between the outermost edges of the perpendicular projection of the shrub and tree canopies, while the shrub and tree layer were defined as all woody vegetation between 1-7 m and > 7 m, respectively **(d)** Schematic overview of the five classes used to characterize the vertical hedgerow structure.

2.4. Data analysis

To test our hypotheses, we adopted a multilevel mixed-effect modelling approach. We fitted univariate linear mixed-effect models (LMM) with restricted maximum-likelihood model estimation ((Zuur et al., 2009)) using the ‘lmer’ function of the ‘lme4’ package ((Bates et al., 2015)) in R Version 3.5.1 ((R Core Team, 2019)). In these models, a random intercept term ‘sensor ID’ was included to account for temporal autocorrelation in temperature measurements of the same temperature sensors. In addition, two random intercept terms ‘region’ and ‘site’ (nested within ‘region’) were also included to account for the hierarchical structure of the dataset and spatial autocorrelation between temperature measurements of the same geographical region or study site. All model assumptions were checked graphically prior to the analyses ((Zuur et al., 2009)), but transformations were not considered necessary following these procedures.

First, we assessed how the magnitude of the temperature offset as well as diurnal temperature range in woodlands and hedgerows changed as a function of distance to the woodland-hedgerow ecotone. We fitted LMMs with ‘temperature offset’ (for daily mean, minimum and maximum temperatures of a full year; calculated as the temperature from our sensors minus the temperature from the corresponding weather stations) and ‘diurnal temperature range’ as response variables and the categorical variable ‘distance’ (relative to the ecotone) as a fixed effect. This procedure was then repeated for summer (June, July, and August) and winter (December, January and February) temperatures. Next, we used a post-hoc (Tukey Multiple Comparisons) test to compare the temperature data of the different sensors along the woodland-hedgerow transects with the ‘glht’ function of the ‘multcomp’ package ((Hothorn et al., 2008)).

Second, we assessed how macroclimate temperatures influenced the variation in the magnitude of the temperature offset in woodlands and hedgerows. As above, we fitted LMMs with ‘temperature offset’ (for daily mean, minimum and maximum temperatures of a full year) as response variable and the interaction between ‘macroclimate temperatures’ and ‘habitat type’ (‘woodland’ or ‘hedgerow’) as fixed effect. If the interaction term tested significant, the dataset was split according to the factor variable ‘habitat type’, and the effect of macroclimate temperatures was analysed for woodlands and hedgerows separately. This procedure was again repeated for summer and winter temperatures.

Third, we tested the effect of canopy structure and composition (canopy cover, height and total cover of the tree and shrub layer, shade-casting ability) as well as hedgerow width and vertical structure (see **Table A.5**) on the magnitude of the temperature offset and diurnal temperature range, specifically for hedgerows. For each of the temperature metrics (daily mean, minimum and maximum temperature offsets and diurnal temperature range) and for each period (full year, summer and winter), we ran a series of separate univariate LMMs with ‘temperature offset’ as response variable and the single site characteristics as fixed effects. For categorical predictor variables, we subsequently used a post-hoc (Tukey Multiple Comparisons) test to compare the temperature data among the different categories of this variable.

3. Results

3.1. Variation in temperature buffering along hedgerow-to-woodland interior gradient

Across all regions, yearly mean and maximum temperatures were on average 0.102 ± 0.049 °C (mean ± SE) and 0.506 ± 0.195 °C higher in hedgerows than in woodlands, while minimum temperatures were 0.239 ± 0.409 °C lower (**Table A.6**). In summer, mean and maximum temperatures were 0.202 ± 0.048 °C and 0.800 ± 0.241 °C higher in hedgerows compared to woodlands, whereas minimum temperatures were 0.336 ± 0.187 °C lower (**Table A.7**). In winter, mean and maximum temperatures were only 0.025 ± 0.003 °C and

0.207 ± 0.021 °C higher in hedgerows, while minimum temperatures were 0.095 ± 0.082 °C lower (**Table A.8**). The diurnal temperature range was 0.685 ± 0.014 °C higher in hedgerows than in woodlands across the whole year. During summer and winter, the diurnal temperature range was respectively 1.04 ± 0.026 °C and 0.287 ± 0.018 °C higher in hedgerows than in woodlands (**Table A.9**). We thus find consistently higher temperature ranges in hedgerows than woodlands.

On an annual basis, mean ($\chi^2 = 30.0$, $P < 0.001$) and maximum temperature offsets ($\chi^2 = 49.5$, $P < 0.001$) increased significantly with distance from woodland interior towards hedgerow, while for minimum temperature offsets ($\chi^2 = 33.2$, $P < 0.001$) a decrease was found (**Fig. 2a** and **Fig. A.2**). In summer, similar patterns were detected, with increasing mean ($\chi^2 = 45.3$, $P < 0.001$) and maximum temperature offsets ($\chi^2 = 52.2$, $P < 0.001$) and decreasing minimum temperature offsets ($\chi^2 = 38.8$, $P < 0.001$) relative to the woodland interior (**Fig. 2b** and **Fig. A.3**). In winter, maximum temperature offsets increased ($\chi^2 = 11.4$, $P = 0.044$) with distance, while minimum temperature offsets decreased ($\chi^2 = 19.2$, $P = 0.002$). Mean temperature offsets during winter showed no significant pattern along the transect ($\chi^2 = 7.06$, $P = 0.216$) (**Fig. 2c** and **Fig. A.4**). The diurnal temperature range increased significantly with distance relative to the woodland interior for all studied time periods (**Fig. A.5** and **Table A.10**).

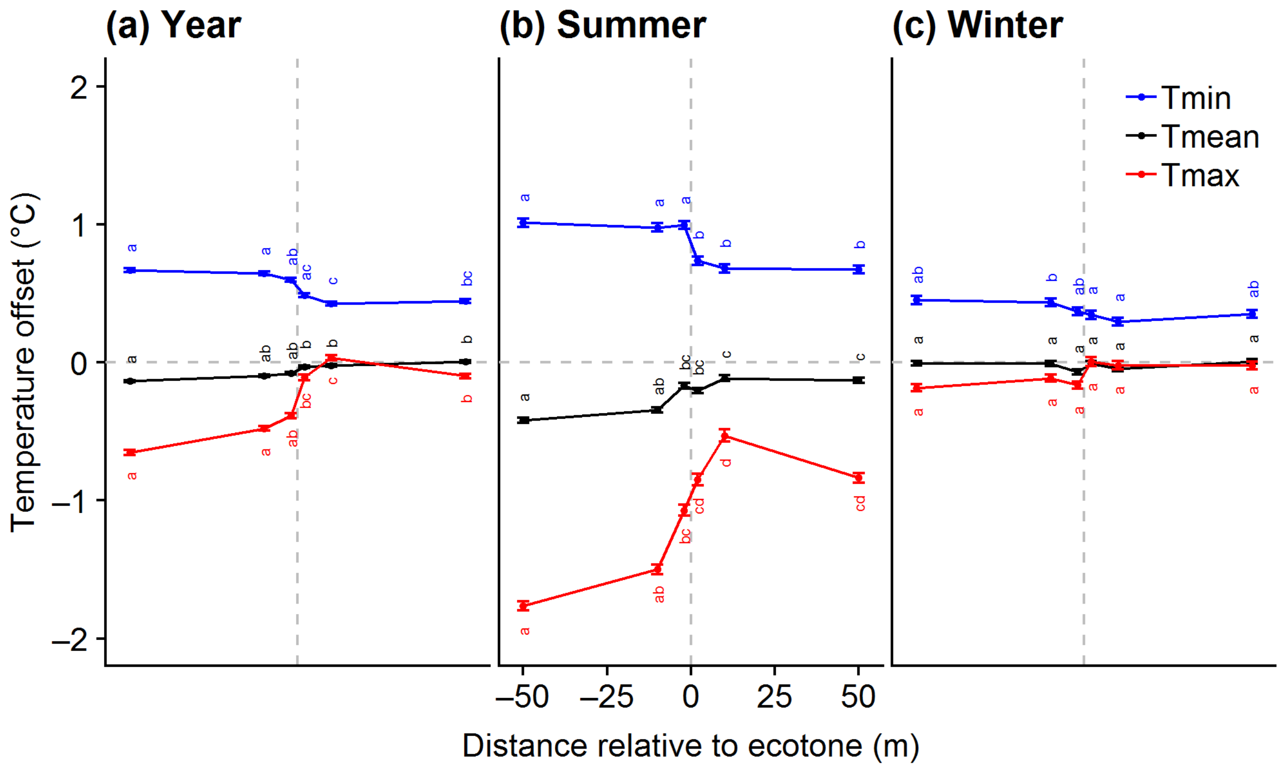

Fig. 2. Distance patterns in temperature buffering. Temperature offset values for minimum (in blue, T_{min}), mean (in black, T_{mean}) and maximum (in red, T_{max}) temperatures as a function of the distance relative to the forest-hedgerow ecotone during a full year **(a)**, during summer (June-August) **(b)** and during winter (December-February) **(c)**. The temperature offset was calculated as sub-canopy (microclimate) minus macroclimate (macroclimate) temperatures; negative (positive) values thus denote cooler (warmer) sub-canopy temperatures. The *dashed horizontal lines* represent the null line (temperature offset = 0 °C). The *dashed vertical lines* show the connection point between forest and hedgerow; positive distances are used for the hedgerow, while negative distances are used for the forest. Error bars represent standard errors of the mean. Different letters denote significantly different values according to a linear mixed-effect model (LMM; $P < 0.05$).

3.2. Effect of macroclimate temperatures on temperature buffering

For all temperature metrics (daily minimum, mean and maximum temperatures), we found a significant negative relationship between macroclimate temperatures and the magnitude of the temperature offset in both woodlands and hedgerows. These patterns were consistent for a full year as well as during summer and winter. Interestingly, particularly for maximum temperatures in summer, the slope of this relationship was significantly more negative in woodlands than in hedgerows, indicating that woodlands provide better buffering than hedgerows at higher ambient temperature maxima, but similar buffering at lower ambient temperature maxima (**Fig. 3** and **Table A.11**).

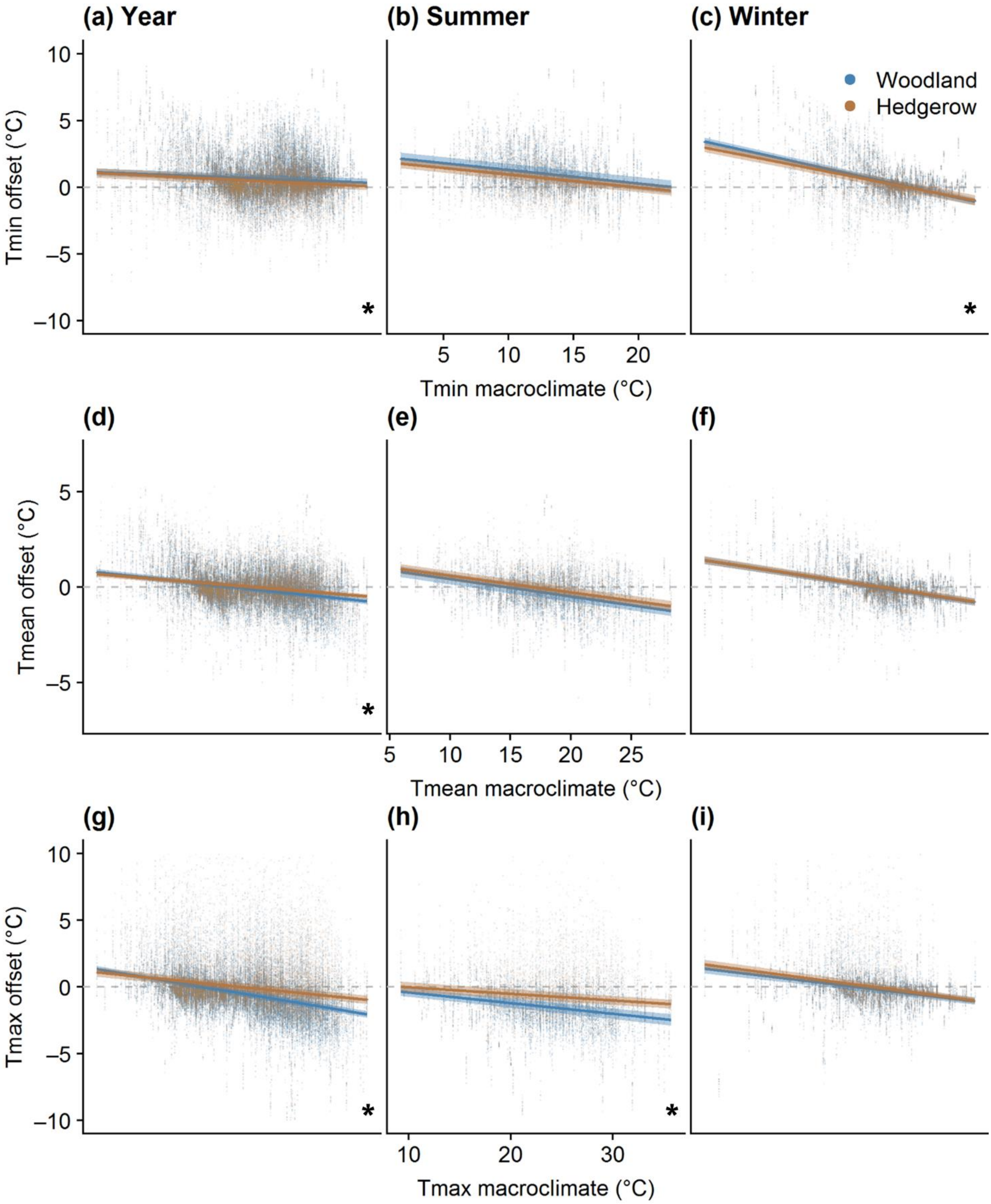

Fig. 3. Effect of macroclimate on temperature buffering. Temperature offset values for minimum (T_{min}), mean (T_{mean}) and maximum (T_{max}) as function of corresponding macroclimate tempertures in woodlands and hedgerows during a full year **(a, d, g)**, during summer (June-August) **(b, e, h)** and during winter (December-February) **(c, f, i)**. The temperature offset was calculated as sub-canopy (microclimate) minus macroclimate (macroclimate) temperatures; negative (positive) values thus denote cooler (warmer) sub-canopy

temperatures. Fitted regression lines and 95 % confidence intervals are from linear mixed-effect models (LMM; $P < 0.05$). The '*' in **(a)**, **(c)**, **(d)**, **(g)** and **(h)** indicates that the interaction term between 'macroclimate temperatures' and 'habitat type' ('woodland' or 'hedgerow') was significant at $P < 0.05$.

3.3. Effect of hedgerow structure on temperature buffering

On an annual basis, we detected a significant cooling effect of canopy cover on daily maximum temperatures in hedgerows ($\chi^2 = 4.51$, $P = 0.034$), while tree height showed a cooling effect on both mean ($\chi^2 = 6.02$, $P = 0.014$) and maximum ($\chi^2 = 5.84$, $P = 0.016$) temperatures. In addition, significantly lower daily temperature maxima were found in wider hedgerows ($\chi^2 = 5.60$, $P = 0.018$). Low, single-storied (only shrub layer) hedgerows showed smaller minimum temperature offsets than tall, single-storied (only tree layer) hedgerows (**Fig. A.6**, **Table A.12-A.13** and **Table A.16-A.17**).

In summer, we found significant cooling effects of canopy cover ($\chi^2 = 4.55$, $P = 0.033$) and total tree cover ($\chi^2 = 5.29$, $P = 0.021$) on maximum temperatures. A higher total tree cover also resulted in a smaller diurnal temperature range ($\chi^2 = 7.06$, $P = 0.008$). Mean ($\chi^2 = 4.19$, $P = 0.041$) and maximum temperatures ($\chi^2 = 4.35$, $P = 0.037$) were more buffered below taller trees, while shrub height positively affected mean temperature offsets ($\chi^2 = 4.28$, $P = 0.038$). Maximum temperature offsets during summer were again lower in wider hedgerows ($\chi^2 = 5.13$, $P = 0.024$). Low, single-storied hedgerows showed smaller minimum temperature offsets than tall, single-storied hedgerows (**Fig. 4**, **Table A.14-A.15** and **Table A.16-A.17**).

During winter, tree height showed a significant cooling effect on mean temperature offsets ($\chi^2 = 4.44$, $P = 0.035$) (**Fig. 4**, **Table A.14-A.15** and **Table A.16-A.17**).

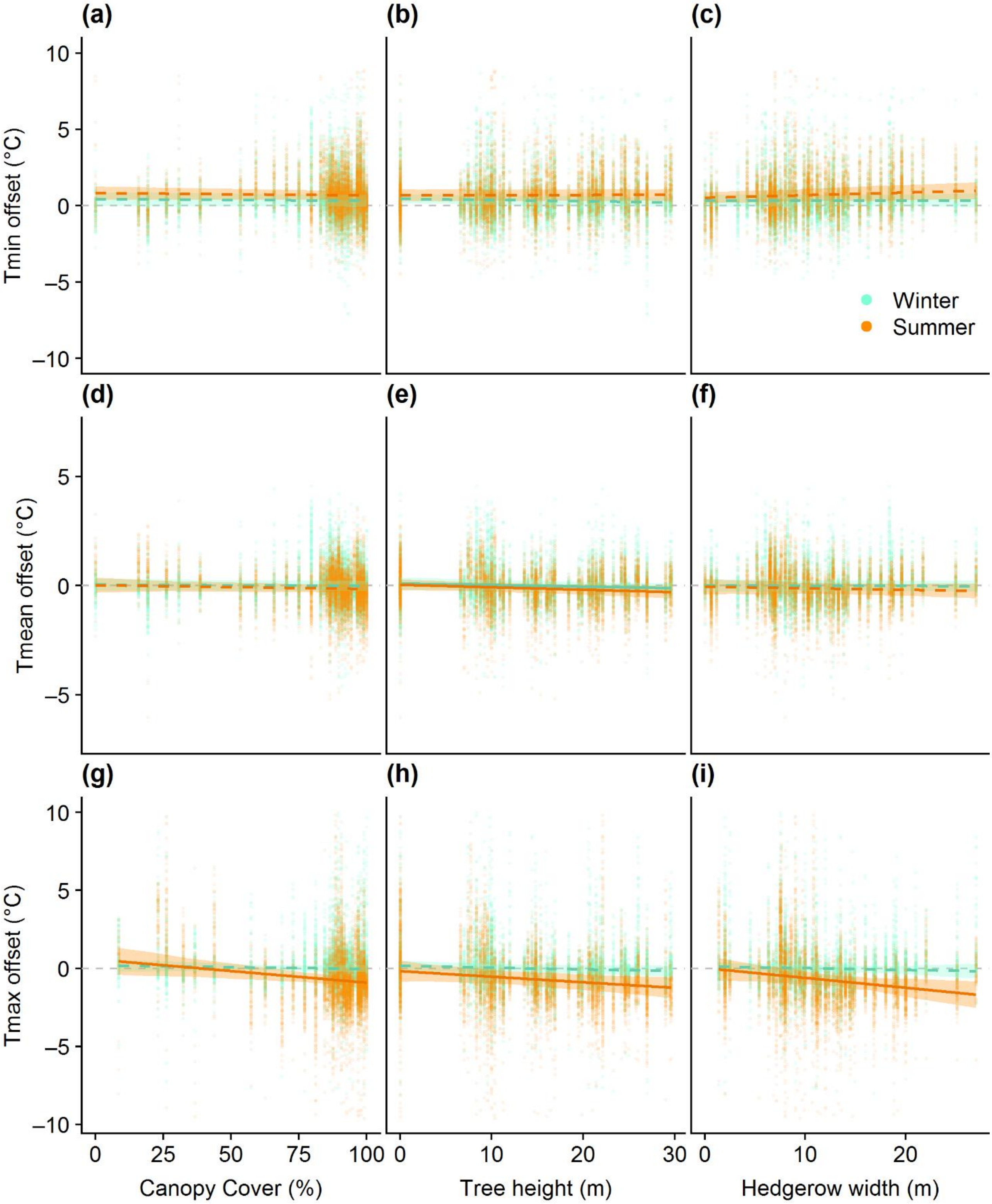

Fig. 4. Effect of site characteristics on temperature buffering. Temperature offset values for minimum (T_{min}), mean (T_{mean}) and maximum (T_{max}) summer and winter temperatures in the hedgerows as function of canopy cover **(a, d, g)**, tree layer height **(b, e, h)** and hedgerow width **(c, f, i)**. The temperature offset was calculated as sub-canopy (microclimate) minus macroclimate (macroclimate) temperatures; negative (positive) values thus denote cooler (warmer) sub-canopy temperatures. Fitted regression lines and 95 % confidence intervals

are from linear mixed-effect models (LMM). *Dashed lines* are not significant, while *solid lines* are significant at $P < 0.05$.

4. Discussion

Using a unique dataset of sub-canopy temperatures in woodlands and hedgerows across temperate Europe, we show that the thermal buffering capacity of hedgerows is lower than that of woodlands, particularly during summer. Maximum temperatures in hedgerows were consistently higher, whereas minimum temperatures were lower. Nonetheless, we underpin that temperature buffering in hedgerows can be increased via hedgerow management through modification of several structural attributes, for example, by creating a high and dense canopy and extending the width of hedgerows.

4.1. Variation in temperature buffering along hedgerow-to-woodland interior gradient

Mean and maximum temperatures inside woodland interiors were lower than open-field temperatures, while minimum temperatures were higher. During the day, tree canopies reflect, absorb or transmit the incoming solar radiation. Solar radiation thus diminishes rapidly with depth into the canopy, and this energy is largely converted into latent heat via evaporation of moisture from the ground surface and foliage as well as transpiration through plant's stomata (usually jointly referred to as evapotranspiration). In addition, the canopy, along with tree stems, also reduces the mixing of air due to wind flow, causing cooler and more uniform near-ground thermal conditions ((Chen et al., 1993; Geiger et al., 2009; Li et al., 2015; Murcia, 1995)). During the night, however, woodlands tend to be warmer than open lands ((Chojnacka-Ożga and Ożga, 1999)) due to the attenuation of outgoing infrared radiation by the canopy, allowing woodlands to lose their heat more gradually compared to open areas ((Houspanossian et al., 2012)). Furthermore, the magnitude of temperature buffering decreased from woodland interior towards edge, with the steepest decline occurring within 10 m from the edge. This pattern is in accordance with previous studies (e.g. (Arroyo-Rodríguez et al., 2016; Chen et al., 1993; Chen et al., 1999; Tuff et al., 2016)), and can be explained by the rising influence of edge effects. For instance, increased light availability near woodland edges, particularly due to the lateral transmittance of incident light entering through the canopy, is likely an important mechanism driving these temperature changes ((Davies-Colley et al., 2000)).

The magnitude of temperature buffering decreased even further in the hedgerows, with a distinct peak in maximum midday temperatures around 10 m from the woodland edge. Interestingly, after this point buffering increased again and maximum temperatures at 50 m in the hedgerow did not statistically differ from the woodland boundary. One potential explanation for this pattern could be that hedgerows act as a wind barrier, causing considerably lower wind speeds at the bottom of hedgerows (especially at the leeward side of the corridor; (Forman and Baudry, 1984)). In turn, this could result in a reduction of air mixing and evaporation, leading to higher daytime temperatures both inside and directly adjacent to the hedgerow ((Geiger et al., 2009)). Wind speeds are presumably most attenuated close to the connection point with the woodland, and together with the declining thermal buffering effect of the nearby woodland, this could account for the observed temperature peak at 10 m in the hedgerows. Conversely, during the night, the reduction of wind speeds and resulting air mixing implies that less warm air will be transported down from aloft, causing lower nocturnal temperatures in hedgerows than in nearby woodlands. As expected, we found similar patterns for the diurnal temperature range, with higher differences between daily maximum and minimum temperatures in hedgerows than in forests. However, it was striking that the differences were highest again at 10 m into the hedgerow, with smaller temperature ranges observed further along the corridor.

4.2. Effect of macroclimate temperature on temperature buffering

In general, the temperature offset of the woodland patches became more negative (i.e. lower temperatures in woodlands) as ambient temperatures increased and more positive (i.e. higher temperatures in woodlands) as ambient temperatures decreased. Together, these results imply that woodlands act as thermal insulators, thereby moderating the negative impact of macroclimatic warming on organisms living below tree canopies ((De Frenne et al., 2013; Renaud and Rebetez, 2009)). Microclimatic buffering in hedgerows was also negatively correlated to macroclimate temperatures, but the slope of this relationship was markedly lower for temperature maxima. Thus, particularly on warm summer days, hedgerows will be less efficient thermal insulators than woodlands. These conditions could negatively affect the long-term survival of forest-adapted organisms in hedgerows, notably due to the increased risk of their thermal tolerance limits being exceeded by extreme temperature events.

4.3. Effect of hedgerow structure on temperature buffering

The moderating effect of canopy closure on microclimate temperatures in hedgerows, particularly during summer, is in line with our expectations. Denser tree canopies reduce the transmission of solar radiation to the understorey and diminish the penetration of turbulent eddies through the foliage induced by wind flow over the canopy ((Bonan, 2015; Campbell and Norman, 1998; Chen et al., 1993)). The cooling effect of tree height is potentially coupled to this canopy effect; higher tree crowns generally provide more overstorey cover. Indeed, Martens et al. (2000) reported that light transmission to the understorey of woodland stands was negatively related to tree height. Alternatively, high and dense tree canopies also form a thicker boundary layer between atmosphere and understorey, resulting in a stronger decoupling from the surrounding macroclimate ((Benítez et al., 2015; Martens et al., 2000)). Tall forest vegetation is also aerodynamically rough, has a high aerodynamic conductance, and dissipates the incoming solar energy more efficiently compared to short vegetation ((Bonan, 2015)). Furthermore, we detected a positive effect of hedgerow width on the magnitude of buffering. Indeed, due to the declining influence of edge effects, we expect the interior part of wider hedgerows to be characterized by a more woodland-like microclimate (cf. (Roy and de Blois, 2008; Wehling and Diekmann, 2007)).

4.4. Implications for management and biodiversity conservation

Fine-scale climatic variations play a major role in shaping plant distribution patterns across space and time ((Ashcroft et al., 2009; Geiger et al., 2009)). Therefore, microclimates can be used as a regulating service to steer the colonization of species such as woodland specialists in hedgerows, and enhance their effectiveness as movement corridors between isolated habitat patches. Additionally, if the microclimatic conditions are favourable, hedgerows may provide a refuge habitat for woodland-dwelling species in landscapes with relatively few woodland patches. Indeed, studies (e.g. (Corbit et al., 1999; Wehling and Diekmann, 2009)) have shown that woodland specialists are more likely to occur in wider hedgerows with a well-developed tree canopy, most likely due to the more benign microclimatic conditions therein. Ultimately, hedgerows may also be crucial to ensure the long-term survival and dispersal of woodland-dwelling species under climate change, by providing a suitable microenvironment that partially resembles woodland conditions and may thus potentially alleviate their response to global warming ((Lenoir et al., 2017)). Even so, it should be noted that the thermal buffering capacity of these woody habitats will likely change over time with changes in the macroclimate, having important implications for their biodiversity and associated ecosystem functions ((Arnone et al., 2008; Davis et al., 2019)).

Furthermore, a thorough understanding of the microclimatic conditions in hedgerows is of paramount importance to landscape managers and policy makers, because it helps when making decisions to maximize biodiversity conservation and ecosystem service delivery in these linear habitats, acting as effective environmental corridors and potential microrefugia for many species groups. Management practices that lead to more effective buffering of the understorey microclimate in hedgerows could significantly benefit the long-term colonization success of species in these woody corridors. In particular, wider hedgerows with substantial lateral crown cover and a tall, dense tree canopy are expected to create more buffered microclimatic conditions, which may in turn promote the establishment and migration of temperate woodland species. Potential strategies are to relax the cutting regime and allow hedgerows to incrementally increase in height. Meanwhile, the effect of wind could also be mitigated by altering the hedgerow structure. Wind is likely an important factor controlling other microclimatic variables such as temperature and relative humidity ((Saunders et al., 1991)), and modulating the wind flow over hedgerows could strongly reduce edge effects. Notably, our results suggested that air temperatures were most extreme in hedgerows around 10 m from the woodland boundary, especially during summer. We therefore propose a more gradual transition between woodland edge and hedgerow, both vertically and laterally (that is, a taller and wider hedgerow close to the connection point), to effectively moderate edge effects (e.g. by reducing the turbulent airflow in the woodland-hedgerow ecotone). However, we acknowledge that the latter should be further investigated with field trials or wind tunnel experiments.

5. Conclusion

As species migrations are predicted to accelerate under climate change ((Walther et al., 2002)) and habitats become increasingly fragmented due to human land-use activities ((Haddad et al., 2015)), hedgerows may play a key role in the long-term conservation of species by providing a temporary refuge habitat or even dispersal route between isolated habitat patches such as woodlands. Yet, the sub-optimal microclimatic conditions, particularly around the connection point with the woodland, could potentially hamper the migration of species into these woody corridors. This leads us to suggest that measures associated with the management, restoration and establishment of hedgerows in rural landscapes should focus on creating a favourable sub-canopy microclimate, which closely resembles the conditions found in woodlands. This could significantly enhance the colonization success of woodland-dwelling species into hedgerows and, to some extent, mediate their response to climate warming.

Acknowledgements

We thank the Research Foundation – Flanders (FWO) for funding the scientific research network FLEUR. TV was funded by the Special Research Fund (BOF) from Ghent University (01N02817), SG by the FWO (G0H1517N), PDF by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833) and KV through ERC Consolidator Grant (PASTFORWARD 614839).

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